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Short communication

The seed ecology of an ornamental wattle in South Africa — Why has *Acacia elata* not invaded a greater area?

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ABSTRACT

Australian *Acacia* species introduced to South Africa as ornamentals have notably smaller invasive ranges than those introduced for forestry or dune stabilization. We asked whether the relatively small invasive extent of *Acacia elata*, a species used widely for ornamental purposes, is due to low rates of reproduction. Age at reproductive maturity, seed dispersal, annual seed production, seed bank dynamics and seed germination and viability were assessed at five sites in the Western Cape. Results indicate that *A. elata* has similar traits to other invasive Australia *Acacia* species: annual seed input into the leaf litter was high (up to 5000 seeds m^{-2}); large seed banks develop (>20,000 seeds m^{-2}) in established stands; seed germinability is high (>90%); seeds accumulate mostly in the top soil layers but can infiltrate to depths of 40 cm; and seed germination appears to be stimulated by fire. However the age at the onset of reproduction (~4 years) is longer than most widespread invaders (~3 years) and dispersal is fairly limited (seeds fell up to distances of 6 m from the parent canopy; the highest density of seed rain was found directly under the canopy with over 20% of seeds falling directly under the terminal branches). We suggest that the current limited distribution of invasive *A. elata* populations is the result of the relatively small size of initial populations (cf. large plantations and widespread plantings for forestry and dune stabilization species), the species' apparent lack of secondary dispersal vectors, and the planting of trees in gardens and urban settings offer limited opportunities for recruitment, proliferation and spread. The species is, however, increasing in abundance and range. We propose methods to improve management of invasions of the species. Management to reduce seed production of this species through classical biological control, as has been achieved for other Australian *Acacia* species in South Africa, should be prioritised.

1. Introduction

Only a small proportion of the very large number of plant species introduced into novel habitats by humans become invasive (Ewel et al., 1999). The limited number of species that establish and spread in novel ranges can largely be attributed to the environmental and manmade barriers to survival, reproduction and dispersal experienced in a new region (Blackburn et al., 2011). Previous studies have shown that reproductive traits related to seed dispersal, seed production, seed size, and the ability to generate long-lived seed banks are consistently linked to the likelihood that introduced trees become invasive (Gibson et al., 2011; Gioria et al., 2012). Developing a comprehensive understanding of the seed ecology of introduced species can provide valuable insights into their invasive potential and how they should be managed.

At least 80 Australian *Acacia* species were introduced and disseminated throughout South Africa over the last 150 years (Poynton, 2009; Le Roux et al., 2011; Richardson et al., 2011). Although the fourteen Australian acacias that are currently invasive in South Africa have been present in South Africa for similar lengths of time, their extents of invasion differ considerably (Nel et al., 2004; Wilson et al., 2007; Van Wilgen et al., 2011). Species introduced for forestry and dune stabilization have much larger invasive ranges and occur in higher abundances in South Africa than those used for ornamentation (Fig. 1). Understanding the reasons for the differences in invasive success is important for developing a robust strategy for managing Australian acacias in South Africa, where some species have yet to colonize large parts of their potential ranges (Rouget et al., 2004). In particular it is important to understand whether those species that were not widely disseminated constitute a substantial invasion debt (sensu Essl et al., 2011) which will require special consideration in strategic planning (Van Wilgen et al., 2011). Alternatively, the differences observed in invasion extent might be due to differences in seed production and dispersal, two of the key determinants of Australian acacia invasions (Richardson and Kluge, 2008).

The reproductive ecology of Australian acacias widely used in forestry and dune stabilization in South Africa has been well studied (Milton and Hall, 1981; Richardson and Kluge, 2008; Marchante et al., 2010; Gibson et al., 2011; Strydom et al., 2011), but such information is lacking

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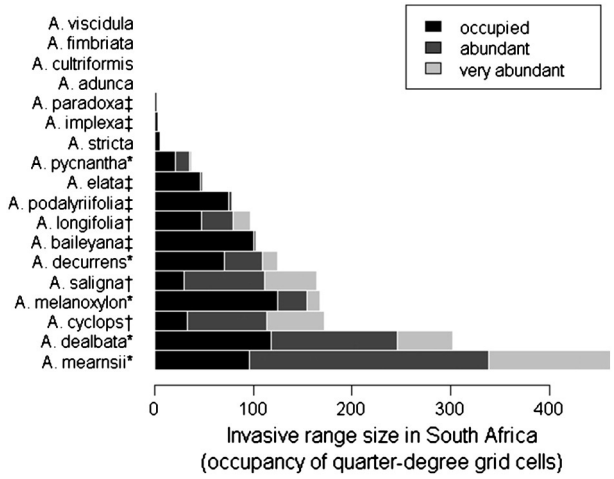

Fig. 1. Invasive Australian *Acacia* species introduced to South Africa and disseminated for use in forestry* and dune stabilization† tend to have the largest invasive distributions and be present at the highest densities when compared to species introduced and disseminated as ornamentals‡ (species reason for introduction and dissemination taken from Wilson et al., 2007, those without symbols were only introduced to a small number of localities for forestry trials; the top four species are only known from single localities).

for species used primarily for ornamentation. In this paper we assess key aspects of the seed biology of *Acacia elata* (A. Cunn. Ex Benth.) and compare the outcome to previous work on traits associated with the success of other invasive *Acacia* species (Richardson and Kluge, 2008; Gibson et al., 2011). Is the limited extent of invasive populations of *A. elata* in South Africa due to inherent reproductive limitations or due to introduction history? The species was selected for this study due to its introduction and dissemination history, the current lack of any introduced classical biological control agents (Impson et al., 2011), and the low current occupancy of its potential distribution (Mgidi et al., 2007; Donaldson et al., 2014b).

2. Methods

2.1. Study species

A. elata is an evergreen, bipinnate tree which under favourable conditions can attain a height of more than 20 m (Poynton, 2009). It has an extensive natural distribution in south-eastern Australia and Tasmania, growing best in warm, humid conditions (Poynton, 2009). The size of the tree, its dark green leaves, and its yellow flowers arranged in racemes make it "Unquestionably one of the handsomest of all the Australian [*Acacia*] species… when at its thriftiest, verges in appearance on the majestic" (Poynton, 2009). The species was introduced to southern Africa as an ornamental species on several occasions between 1904 and 1940. Plants were often planted by foresters around forestry offices for ornamental purposes but were also disseminated by nurseries across the country. Introductions were haphazard and spread throughout the region, with small scale plantings in the Western Cape, Eastern Cape, Free State, Gauteng, KwaZulu-Natal and Zimbabwe (Poynton, 2009; see also Donaldson et al., 2014a). The species has since naturalized and become invasive in many regions of the country and is at present considered a substantial threat (50% of southern Africa is climatically suitable, but the species is only found in 4.5% of this suitable range) (Nel et al., 2004; Mgidi et al., 2007). Given its invasion potential, but the fact that large trees are planted for ornamentation, it is currently listed under category 3 of the Conservation of Agricultural Resources Act (Act 43 of 1983), i.e. no new plants may be planted, but existing trees need not be removed.

Surveys in Australia attempting to find a host specific biological control agent for this species have so far been unsuccessful (Impson et al., 2011). Biological control agents released against other *Acacia* species have the potential to affect *A. elata*, but the lack of a species-specific control agent to date means that land managers are limited in their ability to restrict future dispersal events (Impson et al., 2011).

2.2. Study site

Five *A. elata* stands on flat gradients were selected within the Western Cape, South Africa. Sites were selected with a range of disturbance histories and with different stand ages (Table 1).

2.3. Age at sexual maturity

To estimate age at first reproduction, we cut down fifty of the smallest trees (i.e. those likely to be the youngest in an invaded area) that had reproductive organs present, and counted age rings.

2.4. Seed rain and seed dispersal experiments

Both the seed dispersal and seed rain experiments utilized the seed traps described in Cottrell (2004). Two-litre plastic bottles were cut and the top end inverted and placed in a PVC pipe for support. A mesh bag was attached to the open lid of the bottle to create a net into which seeds were funnelled. The PVC pipes were placed in the field and supported with steel pegs to restrict movement (Cottrell, 2004).

At each site, five sexually mature trees were selected for analysis of seed rain. The height, canopy width, diameter at basal height (DBH) and position of every tree were recorded. Five seed traps were placed at the edge of the canopy of each tree, the first trap facing north and the other four traps arranged at 72° intervals around the canopy of the tree. Traps were set at all sites prior to seed rain (pre-dehiscence), in late August 2012, and were checked every fortnight to limit seed loss due to predation until post-dehiscence when traps were collected in early January 2013.

As seed-rain measures are counts, generalised linear models (GLM) assuming Poisson errors were used to estimate the log mean seed rain per tree (seeds$\cdot$m^{-2}; Quinn and Keough, 2002). These were then compared using one-way interactions with tree height, DBH and canopy width, with AIC values used to select the best model.

At three of the five sites selected for seed rain analysis, three mature trees with canopy widths of 6 m, similar tree height and DBH were selected for analysis of seed dispersal. Seed rain and dispersal in Australian acacias have been shown to be influenced by the dominant wind direction (Marchante et al., 2010). In this study we were interested in the maximum gravity-driven dispersal distances of *A. elata* seeds and therefore set seed-dispersal traps on transects extending away from the selected trees in the direction of the dominant wind direction. Dominant wind direction was obtained from the closest weather stations to each site (http://www.windreport.co.za), and we used the value for when seed rain was at its peak, i.e. December. Traps were set out in a regular distribution along one transect for each tree (Bullock et al., 2006; Marchante et al., 2010) resulting in three transects at each stand. Following the method of Marchante et al. (2010), the end of the most extreme pod bearing branch was labelled as the zero point with a trap placed at this point. Ten traps were then placed every metre for 10 m along the transect running away from the tree. Another three traps were positioned at 1-m intervals for 3 m towards the base of the tree stand. Two traps were placed 20 m and 50 m along the transect line away from the canopy, resulting in a total of 15 traps per tree. Traps were set at all sites pre-dehiscence, in late August 2012 and checked every fortnight to limit seed loss through predation in traps until post-dehiscence when traps were collected in early January 2013.

Seeds per trap were converted to seeds$\cdot$m^{-2} and corrected for distance from parent tree by multiplying by area. We analysed the effect of distance from the parent canopy to proportion of seed rain by regression using a GLM with negative binomial errors to account for overdispersion. The relationship between tree height and seed rain

Table 1
Measurements of seed ecology at five *Acacia elata* stands in the Western Cape.

	Latitude	Longitude	Habitat description	Stand age (years)	Last fire	Wind[a]	Mean tree height (m)	Tree density (m^2 wood/ha)	Seed rain (seeds·m^{-2})	Seed density pre-dehiscence (seeds·m^{-2})	Seed density post-dehiscence (seeds·m^{-2})	Seed bank (seeds.m^{-2})	Estimated annual input[b] (seeds·m^{-2})
Warwick farm	−33.8442	18.8639	Road side	20+	Not known	SE	14.46	428	360 (110–610)	1806 (911–3450)	3388 (2620–4292)	21,171 (17,689–25,631)	1375
Lourensford 1	−34.0266	18.91177	Pine plantation	5	2009	SE	10.20	431	393 (106–679)	358 (196–634)	975 (793–1183)	287 (220–366)	536
Lourensford 2	−34.0258	18.90754	Pine plantation	5	2009	SE	5.60	395	97 (37–157)	315 (135–697)	559 (405–748)	96 (62–140)	332
Lanzerac farm	−33.9591	18.9163	Riparian	20+	Not known	SE	9.20	355	363 (111–617)	110 (31–307)	1027 (778–1326)	167 (109–244)	797
Spanish farm	−34.0523	18.85765	Pine plantation	30+	Not known	SE	16.20	427	767 (388–1145)	2303 (1019–4893)	5725 (4303–7429)	19,160 (14,958–24,082)	2974

[a] Dominant wind direction for December when seed dispersal trapping was undertaken estimated from the closest weather stations available at http://www.windreport.co.za.
[b] Annual input is given by annual seed addition (post-dehiscence leaf litter minus pre-dehiscence leaf litter) to leaf litter minus seeds spontaneously germinating or unviable.

was then used in conjunction with the percentage of seeds falling directly under the terminal branches of the canopy to estimate the total number of seeds released by a single tree of a given height.

2.5. Seed bank dynamics

Seed bank sampling took place at all five sites pre- and post-dehiscence (August 2012 and January 2013 respectively). To get the most accurate sample of the seed bank with reference to size and spread, random soil samples were collected under the canopies of the five different stands, following the approach developed by Strydom et al. (2011). Fifty samples were taken (no closer than 10 m to one another) using a cylindrical corer with 7.2 cm girth down to a depth of 40 cm at each site. The samples were divided into 10 cm depth classes i.e. 0–10 cm, 10–20 cm, 20–30 cm, and 30–40 cm, and kept separately. Each soil sample was sieved through 2 mm mesh and the seeds collected and counted. At each sampling position, the associated tree density was calculated using a wedge prism (Jorgen and Karsten, 1994).

As few seeds were found at depths below 10 cm, for comparisons between sites data for all depths were combined. The number of seeds pre- and post-dehiscence was compared using GLMs with negative binomial errors to cope with overdispersion (Crawley, 2003) for both the seed bank and leaf litter with ANOVAs run to test for significance with any relationships found. All data analysis was carried out using R3.0.1 (R Core Team, 2013).

Only sites at Warwick and Spanish farms had enough seeds below 10 cm to allow for comparisons of seed numbers at different depths. For these sites generalised linear mixed models with Poisson errors were created with depth as the fixed effect and the core number as random effects. ANOVAs were run to test the significance of any relationship found (Quinn and Keough, 2002).

2.6. Seed germinability and viability

Seeds were collected from both seed rain (fresh) and seed bank (soil stored) experiments and used to test seed germinability, viability and response to fire stimulation. One hundred seeds from the seed rain traps and 100 seeds from soil stored seed for each site were washed with bleach (5%) to avoid fungal infection, and then placed in sterilized glass petri dishes on water soaked filter paper kept at a constant 25 °C. Rotten and germinated seeds were removed every two days for 30 days. After this period, any remaining seeds were considered dormant. The micropylar end of dormant seeds was then cut and seeds left as before until they either rotted or germinated. This process was repeated twice, once with water replaced by smoke primer purchased from the South African National Biological Institute, and a second time with boiling water to simulate conditions during fire, which has been shown to break the dormancy of other invasive *Acacia* species (Brown et al., 2003). Seed germinability for the three different treatments and two seeds sources was compared using a GLM with binomial errors.

3. Results

3.1. Age to sexual maturity

Of the fifty trees cut down to estimate the age at onset of reproduction, ten were found to be 4 years old, while the other forty trees were older. This suggests that *A. elata* at the site studied starts reproducing at four years.

3.2. Seed rain and dispersal

As expected, the greatest density of seeds was recorded directly under the canopy close to the stem (Fig. A.1), with seed density declining significantly with increasing distance from the canopy (ANOVA $p < 0.01$). No seeds were found more than 6 m from the canopy edge. However,

after correcting for area, the highest proportion of seed rain was directly under the terminal branches of the canopy (Fig. 2). Of the seed falling outside of the canopy, 50% of the seed was estimated to fall within 3.85 m of the canopy (95% CI 3.04–5.25 m) while only 5% falls further than 16.64 m (95% CI 13.14–22.69, Fig. 2).

There was a significant relationship between seed rain and tree height ($R^2 = 57.02$, $p < 0.001$), DBH ($R^2 = 46.41$, $p < 0.001$) and canopy width ($R^2 = 37.23$, $p < 0.001$), with tree height having the greatest explanatory power (Fig. A.2). We estimate that an average 9 m tree in the Western Cape releases around 17,000 seeds per annum with large trees (>20 m) releasing over 50,000 seeds per annum and small trees (3 m) around 10,000 seeds per annum. The mean seed rain varied between sites from ~100 to 800 seeds·m^{-2} (Table 1).

3.3. Seed bank dynamics

Leaf litter seed counts increased on average from 804 seeds·m^{-2} (95% CI 571 to 1136 seeds·m^{-2}) pre-dehiscence to 1826 seeds·m^{-2} (95% CI 1300 to 2568 seeds·m^{-2}) post dehiscence (ANOVA $p < 0.01$) (Table 1).

The same relationship was not observed in the seed banks, and no significant relationship was observed between pre- and post-dehiscence seed numbers (ANOVA $p > 0.05$). Only one site (Spanish farm) had seeds down to a depth of 40 cm (Fig. A.3), with the majority of seeds found in the top 10 cm of the soil (ANOVA $p < 0.01$, Fig. A.3). The highest recorded density for a single square metre was 95,971 seeds·m^{-2}.

3.4. Seed germinability and viability

There was no significant relationship between seed germinability and viability and site (ANOVA $p > 0.05$). An average of 10.4% seeds that fall spontaneously germinates compared to 2.8% of seeds in the seed bank (ANOVA $p < 0.05$). Smoke water had no significant influence on germination (ANOVA $p > 0.05$); however treatment with boiling water resulted in 77% of seeds in the seed bank and seed from seed rain germinating (ANOVA $p < 0.01$). Mean seed viability for all treatments and sites was 97%.

4. Discussion

High seed rain within dense stands of *A. elata* results in high annual seed input into the leaf litter, which, combined with high seed viability and high levels of dormancy, creates large seed banks of similar proportions to those of other invasive *Acacia* species in South Africa (Richardson and Kluge, 2008; Table 2). Of all reproductive traits of *Acacia*, persistent large seed banks pose the greatest difficulty to management and play a substantial role in the ability of invasive populations to respond to natural and management driven disturbances (Richardson and Kluge, 2008; Wilson et al., 2011). Thus, it appears that the reproductive traits of *A. elata* are consistent with the species becoming an increasingly widespread and abundant invasive species in South Africa.

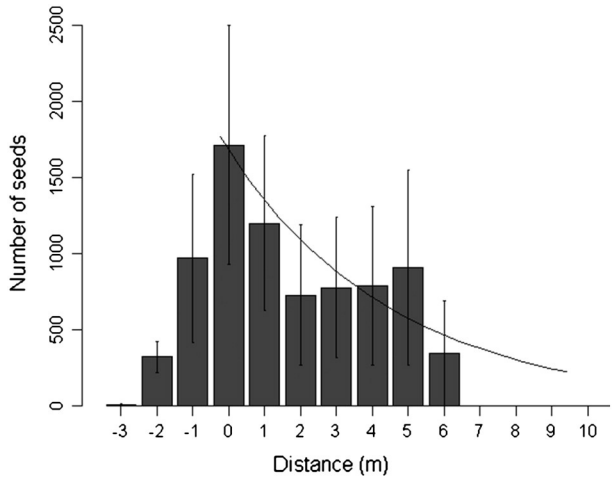

Fig. 2. Seed fall at different distances from the terminal branches (0 m) of *Acacia elata* canopies (error bars represent 95% CI). The black line represents the modelled relationship between distance and seed fall from the edge of the canopy outwards.

4.1. Age to sexual maturity

One difference between *A. elata* and other invasive acacias is that *A. elata* has a longer juvenile period (~4 years). Gibson et al. (2011) report that *Acacia* species that are able to attain maturity within two years of germination were more likely to become invasive than those that are not. It is possible that the longer time to reach reproduction has slowed the rate of establishment of new *A. elata* populations. The time between emergence and reproduction also means that preventing future seed production at a site post-clearing is easier; post-clearing follow-ups can be less frequent.

4.2. Seed rain

The highest recorded mean seed rain for this study (767 seeds·m^{-2}) was within the range reported for two of the most invasive Australian *Acacia* species in South Africa: *Acacia saligna* (530) and *Acacia cyclops* (1197) (Milton and Hall, 1981). However, all sites but one examined in this study showed annual seed rain an order of magnitude lower than those recorded for *A. saligna* in the Western Cape by Strydom (2011). It is possible that either pollination (Parker, 1997) or environmental conditions (Strydom, 2011) are limiting the development of seed in the stands assessed in this study. However, our estimates of the annual seed production of individual trees (10,000–50,000 seeds·yr^{-1}) are within a similar range to those estimated by Milton and Hall (1981) for Australian *Acacia* seed production in the Western Cape: 9500–48,000 seeds·yr^{-1}. This is likely the result of the large canopies and substantial height of *A. elata* trees which would result in a broad dispersal shadow. Consequently, despite the low density of seeds recorded at the terminal branches, the overall input of seeds from individual trees remains substantial, as seeds falling directly under the terminal branches represent a relatively small percentage (<20%) of total seed rain. This is supported by the high seed densities that we noted close to the stem, suggesting that traps placed closer to the stem of the tree would have given greater seed rain densities than those that were measured directly under terminal branches. In addition, seeds captured at 6 m from the edge of canopies suggest seed shadows larger than those recorded for the highly invasive *Acacia longifolia* in Portugal (Marchante et al., 2010), though this is hardly surprising given that mature *A. longifolia* trees are about half the size of mature *A. elata* trees. This does mean, however, that large trees grown in protected gardens for long periods can act as seed sources.

4.3. Seed dispersal

Seed dispersal results indicate that the majority of seeds fall within 4 m of the parent canopy while only 5% of seeds are dispersed beyond 20 m. In reality the seed shadow is likely larger than this, as detection of seed fall at distances further then 10 m was highly unlikely given the low number of traps placed at greater distances (Pielaat et al., 2006). Seed dispersal plays a critical role in determining the speed of invasive spread (Kot et al., 1996) and it is likely that the potential to disperse seeds over relatively large distances purely through gravity will have played a role in the escape from cultivation and spread of *A. elata* in South Africa. However the distances recorded here are far lower than those associated with secondary movement of seeds by birds and mammals observed in other invasive *Acacia* species (>100 m; Glyphis et al., 1981). The white arils on seeds suggest that dispersal by ants is possible (O'Dowd and Gill,

Table 2
The two largest seed banks and seed rain sites recorded for *Acacia elata* compared with the maximum recorded values of seed rain and seed banks of other invasive Australian *Acacia* species in South Africa (data for other species from Richardson and Kluge, 2008).

Species	Seed rain			Seed bank			Estimated accumulation time for mean seed bank (years)
	Annual seed rain (seeds·m^{-2}) [a]	Viability (%)	Dormancy (%)	Seed density (seeds·m^{-2})	Viability (%)	Dormancy (%)	
Acacia elata (Warwick farm)	1582	97	90	21,171	97	97	19
Acacia elata (Spanish farm)	3422	97	90	19,160	97	97	10
Acacia cyclops	1977	100	90–98	5100	99	99	11
Acacia longifolia	11,500	–	96	34,000	97	98	
Acacia mearnsii	–	–	–	5314	83	–	8
Acacia melanoxylon	3200	–	–	43,739	70	–	25
Acacia saligna	5443	98	97	46,000	96–97	96	8

[a] Annual seed rain for other studies was done at the stand level using seed traps, to allow for comparison, and seed rain at the stand level for *A. elata* was estimated from the difference between post- and pre-dehiscence leaf litter seed densities.

1986), but this is unlikely to add to the overall dispersal distances of seed (Bond and Slingsby, 1983; Holmes, 1990; Richardson et al., 2000). In addition, long-distance dissemination of propagules is crucial for driving regional-scale spread of invasive plant species (Higgins and Richardson, 1999); such dissemination is much more likely to be facilitated by human-aided dispersal than by natural dispersal (Pauchard and Shea, 2006). Consequently, although a lack of a secondary disperser may play a role in the population growth at the stand level, the limited dispersal and spread of *A. elata* at regional and national scales is almost certainly more the result of limited human dissemination than limited inherent dispersal capacity. Taking this into account, observations at three sites with trees growing up to 2 km from the main invasion foci with no other seed source in the area, suggest that unintentional human movement of seeds in the area is still playing a role in the spread of the species. All these sites are in or near pine plantations. Dispersal to these sites was probably due to movements resulting from harvesting, planting and road maintenance activities associated with commercial forestry; this has been demonstrated for another Australian *Acacia* (*Acacia stricta*) in the Western Cape (Kaplan et al., 2014). Similar observations at the Lanzerac farm site (within a riverbed) will more likely be driven by the movement of buoyant pods downstream. These propagules are of the greatest concern to management as their detection and removal have the largest impact on effective containment and/or eradication of populations (Panetta, 2009; Moore et al., 2011). Another Australian acacia with a limited invasive distribution in the Western Cape (*Acacia implexa*) was shown to disperse over long distances along a river (Kaplan et al., 2012). The limited distance over which seeds are naturally dispersed means that the movement of seeds over long distances will require secondary dispersal pathways and these will ultimately play a greater role in the overall spread of the species.

4.4. Seed bank dynamics

The seed banks found for *A. elata* are similar in proportions to those of the other invasive Australian *Acacia* species in South Africa. Smaller seed banks at the two Lourensford sites and the Lanzerac site can be attributed to recent fires (young stand age) and flooding within the river system respectively.

4.5. Limits to current invasive distribution

Limitations to spread resulting from limited plantings and placement of these initial introduction foci within gardens as opposed to open landscapes (as was the case for species used for forestry or dune stabilization) are more likely to explain its limited extent. However, the longer the species is allowed to persist without any form of control, the more likely that both deliberate and unintentional regional movement of the species will occur, resulting in increased spread and greater economic costs to management.

4.6. Recommendations for management

Our findings indicate that young stands have limited seed banks. If the goal is extirpation at localized sites, plants should be cleared, a heat treatment used to stimulate seed-germination, and follow-up clearing done within four years (Milton and Hall, 1981; Richardson and Kluge, 2008). It is, however, unlikely that more established stands with large seed banks could be extirpated (Richardson and Kluge, 2008). In such cases, containment may be the best option. The long pre-reproductive period, and the ease with which sexually reproductive trees can be identified, make such a management approach feasible. Populations in areas close to disturbed landscapes with periods of high human activity (e.g. pine plantations during harvest) and those near water courses should receive the most intensive management. In such cases the seeds that have moved downstream will cause the greatest concern and areas downstream should receive surveillance to ensure that new populations do not appear. In order to limit the establishment of new invasive populations the problem of large seed-producing trees on private properties close to land suitable for spread needs to be addressed. A biocontrol agent that reduced seed production would be highly valuable, both for limiting the build-up of seed banks, and for reducing the rates of spread, thus reducing the conflict of interest occurring between conservationists and tree growers.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.sajb.2014.05.004.

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Supporting Information

Fig.A.1 Seed rain density (seeds.m^{-2}) at different distances from the terminal branches (0m) of *Acacia elata* canopies (error bars represent 95% CI).

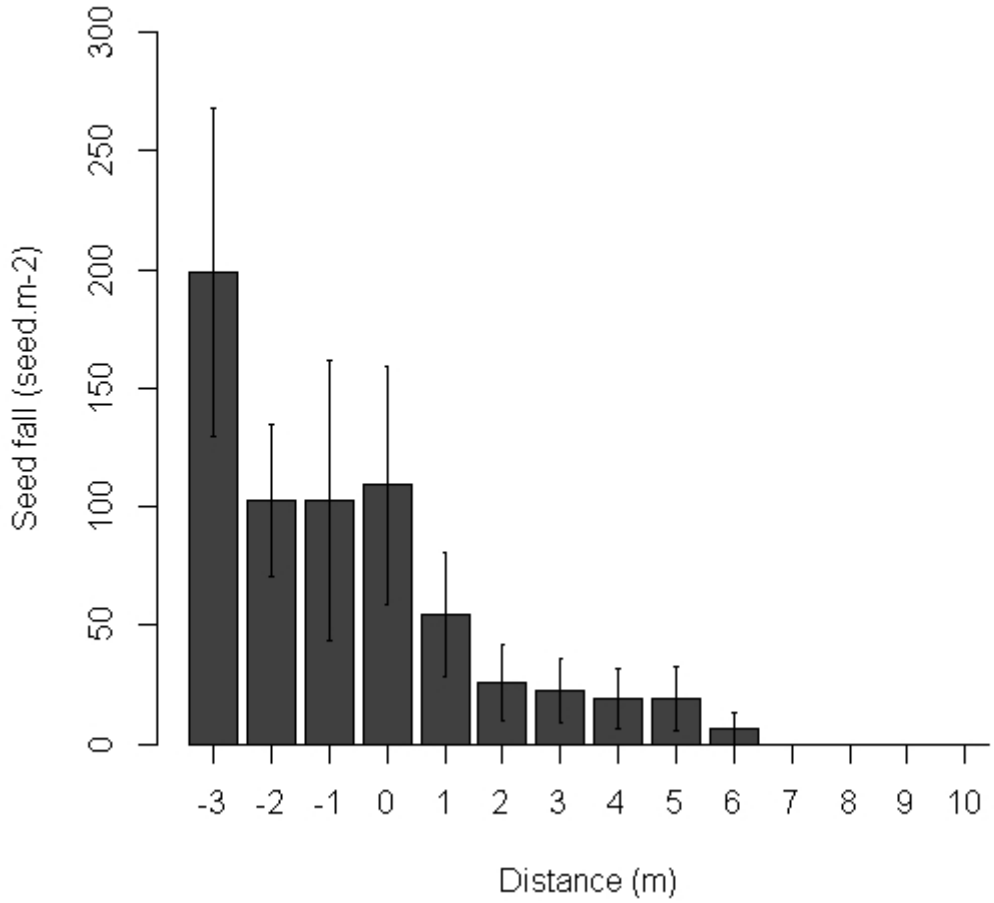

Fig.A.2 Relationship between seed rain and tree height of twenty five *Acacia elata* trees growing in the Western Cape, South Africa, indicating an increase in seed production with greater height (R^2=57.02, P<0.001)

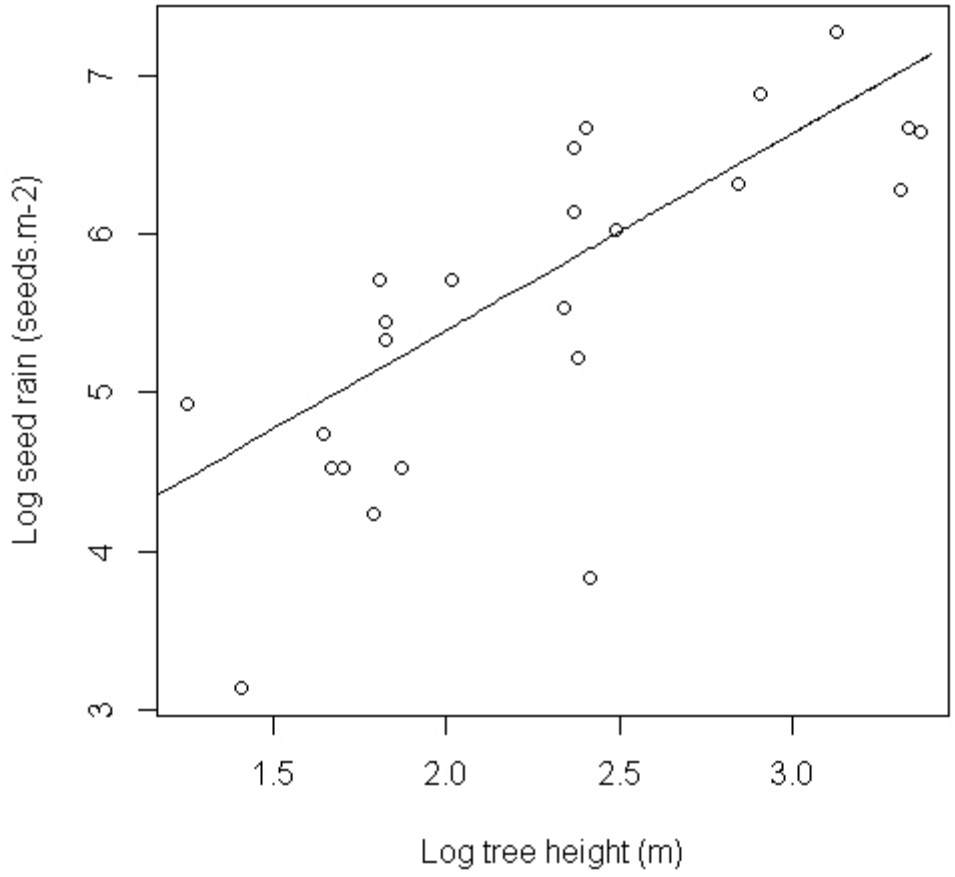

Fig.A.3 Log mean seed density of seedbanks found underneath *Acacia elata* stands at the four different depths analysed for the Warwick farm and Spanish farm sites (error bars represent 95% confidence intervals)